Mediterranean Marine Science

Vol 17, No 3 (2016)

Setting an ecological baseline prior to the bottom-up establishment of a marine protected area in Santorini island, Aegean Sea

M. SALOMIDI, S. GIAKOUMI, V. GERAKARIS, Y. ISSARIS, M. SINI, K. TSIAMIS

doi: 10.12681/mms.1802

To cite this article:

SALOMIDI, M., GIAKOUMI, S., GERAKARIS, V., ISSARIS, Y., SINI, M., & TSIAMIS, K. (2016). Setting an ecological baseline prior to the bottom-up establishment of a marine protected area in Santorini island, Aegean Sea. *Mediterranean Marine Science*, *17*(3), 720–737. https://doi.org/10.12681/mms.1802

Research Article

Mediterranean Marine Science
Indexed in WoS (Web of Science, ISI Thomson) and SCOPUS
The journal is available on line at http://www.medit-mar-sc.net
DOI: http://dx.doi.org/10.12681/mms.1802

Setting an ecological baseline prior to the bottom-up establishment of a marine protected area in Santorini Island, Aegean Sea

M. SALOMIDI[1], S. GIAKOUMI[2,3], V. GERAKARIS[1], Y. ISSARIS[1], M. SINI[4] and K. TSIAMIS[1,5]

[1] Institute of Oceanography, Hellenic Centre for Marine Research, Anavissos, Greece
[2] Université Côte d'Azur, CNRS, FRE 3729 ECOMERS, Nice, France
[3] ARC Centre of Excellence for Environmental Decisions, School of Biological Sciences, The University of Queensland, Brisbane, Queensland, Australia
[4] Department of Marine Sciences, University of the Aegean, Mytilene, Greece
[5] European Commission, Joint Research Centre – Directorate for Sustainable Resources, Water & Marine Resources Unit, Ispra, Italy

Corresponding author: msal@hcmr.gr

Handling Editor: Argyro Zenetos

Received: 3 June 2016; Accepted: 6 August 2016; Published on line: 9 November 2016

Abstract

Since 2010, a bottom-up initiative has been launched in Santorini Island (Aegean Sea, Eastern Mediterranean) for the establishment of the first fully protected marine protected area in the Cyclades, aiming at improving fisheries and enhancing responsible recreational uses at sea. Following discussions with local small-scale fishermen and divers, two sites along the southern and south-eastern coasts of the island were suggested as suitable to this end. In 2012, a baseline study was conducted in these areas to assess their state and provide an ecological snapshot that would enable sound designation and monitoring. Several *ad hoc* indices and metrics were applied, taking into account structural and functional features of the upper infralittoral algae and *Posidonia oceanica* seagrass beds. An integrated assessment of the infralittoral fish assemblages and their associated benthic communities was also performed. Our most important findings were: (i) the low total fish biomass and the absence of adult top predators, indicating overfishing; (ii) the overgrazing effects of the abundant alien herbivore spinefoot fishes (*Siganus* spp.), as reflected by the abnormal structure of the algal communities; (iii) the scarcity of indications of pollution or other direct anthropogenic pressures, as indicated by the good environmental status of the *P. oceanica* meadows and the upper infralittoral vegetation; and (iv) the presence of a rich diversity of species and habitats, especially along the Akrotiri Peninsula and the wider volcanic Caldera. These findings provide useful insights on the strengths and weaknesses of the study area and are discussed together with their implications for protection and management.

Keywords: Marine protected area, fish assemblages, benthic communities, rocky infralittoral, *Posidonia oceanica* meadows, ecological indicators, Aegean Sea, alien species.

Introduction

Historical and current overfishing in synergy with multiple other anthropogenic pressures, such as urban pollution and agricultural runoff, has led to the degradation of marine ecosystems across the Mediterranean Sea (Bianchi *et al*., 2012; Micheli *et al*., 2013). This situation is increasingly evident in the typically oligotrophic waters of the Eastern basin and particularly in the marine area of the Cyclades (Stergiou, 2002; Pennewiss, 2004; Giakoumi *et al*., 2012). Declines in fishery resources profoundly affect local fishers but also marine-based tourism, such as SCUBA diving and snorkelling activities that are driven by a strong interest in marine wildlife observation (PISCO & UNS, 2016).

One practical solution to improve local fisheries and promote responsible tourism whilst enhancing nature conservation is the creation of marine protected areas (MPAs). When considering MPAs in either theory or practice, however, a wide variety of concepts and definitions may apply, encompassing practically everything from marine parks established for the protection of threatened or unique species and habitats, vast areas with various levels of protection, or even sites of historical or cultural interest (Agardy, 2000). According to Lubchenco and Grorud-Colvert (2015), MPAs can be distinguished into: lightly protected, where some protection exists but significant extractive activity is allowed; strongly protected, where all commercial activity is prohibited, and only light recreational and subsistence fishing is allowed; and fully protected, also known as “marine reserves” or "no-take zones", where no extractive activities are allowed. Commonly, the primary goal of MPAs is the conservation of marine biodiversity and ecosystems; however, social, economic, and cultural goals can also be central in their designation (Day *et al*., 2012).

A global review synthesizing evidence on the effects of fully protected MPAs across the globe demonstrated that MPAs can contribute to an average increase of 21% in species diversity, 28% in the size of organisms (algae, invertebrate and fish species), 166% in density (number of individuals per unit area), and 446% in biomass (kg per hectare), compared to adjacent unprotected areas (Lester *et al.*, 2009). These percentages, however, refer only to fully protected MPAs where no fishing or other extractive uses are allowed within their boundaries. A necessary prerequisite to detect such positive effects is the successful enforcement and compliance with the rules set within an MPA. When this prerequisite is not met, the MPA effects are substantially reduced or negligible (e.g. Montefalcone *et al.*, 2009; Campbell *et al.*, 2012; Sala *et al.*, 2012; Guidetti *et al.*, 2014).

Up to 2015, more than 1,100 marine areas have been designated as MPAs across the Mediterranean Sea, corresponding to a total area of about 163,000 km² or 6.5% of the basin's surface (PISCO & UNS, 2016). These designations refer to all MPA categories, including the large Pelagos Sanctuary and Natura 2000 marine sites, many of which still lack management plans and authorities. Fully protected marine areas are estimated to barely cover 0.04% of the Mediterranean Sea (PISCO & UNS, 2016). In reality, this percentage is even smaller, considering that even in many fully protected areas of the Mediterranean poaching and other illegal destructive activities still occur (Guidetti *et al.*, 2008; Sala *et al.*, 2012).

Limited funding allocated to nature conservation and enforcement of MPA management measures in most Mediterranean countries (Katsanevakis *et al.*, 2015) can partly explain the high occurrence of poaching in Mediterranean MPAs. In addition, low compliance with the rules of MPAs by local communities might be attributed to the low level of stakeholder engagement in the planning and management process. Traditionally, nature conservation has been a top-down procedure at either national or regional scale. There is now growing consensus among scientists that bottom-up approaches, i.e. involving stakeholders and local communities at an early stage of MPA establishment, is necessary to achieve social acceptance and compliance. These factors can prove to be more crucial for determining the success of an MPA than design factors, e.g. the size of the MPA (Pollnac *et al.*, 2010; Daw *et al.*, 2011; Campbell *et al.*, 2012; Ferreira *et al.*, 2015). In the Mediterranean Sea, there are few cases where stakeholders have been actively involved in MPA planning since the onset of the initiative. Such successful examples are the Marine Park of Côte Bleue in France (Claudet *et al.*, 2006; Leleu *et al.*, 2012) and the Torre Guaceto MPA in Italy (Guidetti *et al.*, 2010), where increased social support and enhanced MPA positive effects have been demonstrated. In light of this evidence, a bottom-up initiative was launched in Santorini Island (Aegean Sea, Eastern Mediterranean) aiming at improving fisheries and enhancing the recreational uses of the area.

At global scale, Santorini is considered an island of unparalleled beauty. More than 500,000 tourists per year visit the island to enjoy its breath-taking volcanic sceneries. This tourism flow, however, has been stretching the island's limits beyond sustainable levels, thus threatening its unique culture and environment (Wadih, 2005). New tourism development paradigms are therefore needed, and in particular such that seek to eliminate negative tourism impacts, preserve and capitalize on the natural and cultural local resources, and maximize benefits for local communities and stakeholders. The ongoing initiative focused on building consensus among small-scale fishers, recreational diving centres, local authorities and the general public for the creation of the first fully protected area in the Cyclades Islands, Aegean Sea (Cousteau *et al.*, 2010). Following lengthy discussions, two coastal areas of relevant interest were eventually suggested as suitable MPA candidates.

A baseline study was then conducted to assess the natural state of these two areas, according to ecological and environmental criteria. Establishing ecological baselines prior to protection has been a major challenge in marine conservation, given that assessment of the status of coastal ecosystems before the implementation of management schemes has seldom been applied in existing MPAs worldwide (Jennings, 2000; Willis *et al.*, 2003; but see Osenberg *et al.*, 2011 for exceptions). Therefore, the scope of our sampling design was to obtain meaningful qualitative and quantitative information on the current ecological state and future potential of the candidate sites. Such information can prove valuable in providing rigid "ecological snapshots" that enable sound MPA designation and allow for future monitoring of management effectiveness.

Materials and Methods

Study area and sampling design

The volcanic Santorini Island complex includes the islands of Thera, Therasia, Nea Kameni, Palia Kameni, and Aspronisi. They all represent the remains of the collapsed volcanic shield and form a ring around a large submarine caldera that was formed around 1600 BC (Nomikou *et al.*, 2014). The study area comprises two main sub-areas along the coasts of Thera Island: Perissa Rock (PR), encompassing a rocky coastline of approximately 2.5 km on the south-eastern coast of Thera Island, between the sandy beaches of Perissa and Kamari villages; and the Akrotiri Peninsula (AK), a 6.5 km coastline stretching along the south-western part of Thera Island (Fig. 1).

A total of 18 sites were surveyed including 4 sites along Perissa Rock (PR-1, PR-2, PR-3 and PR-4), 7 sites along Akrotiri Peninsula (AK-1, AK-2, AK-3, AK-4, AK-5, AK-6 and AK-7), and 7 control sites selected beyond the boundaries of the proposed areas (CT-1 at Megalochori, PK-1 and PK-2 at Palia Kameni, NK-1 at Nea Kameni, AN-1 and AN-2 at Aspronisi) (Fig. 1).

Site selection was based on a systematic random scheme, placed 1 km apart in the case of Akrotiri Peninsula, and 750 m apart in the case of Perissa Rock. Given the specific requirements of the study in terms of suitable depths and habitats, the final site position had at times to

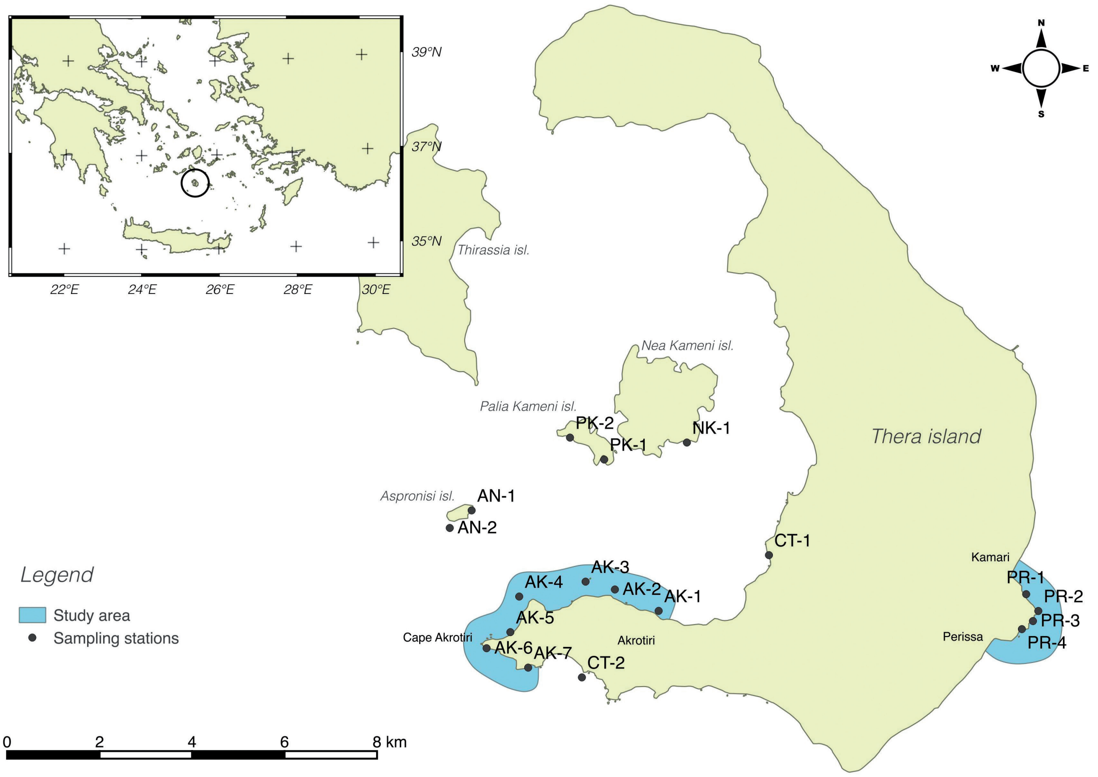

Fig. 1: Map indicating stations along the coasts of Perissa Rock (PR) and Akrotiri Peninsula (AK) (shaded polygons), and several scattered control sites (CT-1, CT-2, NK-1, PK-1, PK-2, AN-1, AN-2).

be slightly readjusted on the spot to ensure habitat presence and continuity.

We focused our research on infralittoral rocky reefs and *Posidonia oceanica* seagrass meadows (Habitat Types 1170 and 1120 respectively, *sensu* the EU Habitats Directive 92/43/EEC), as these habitats support the highest fish biomass in the Mediterranean (Harmelin-Vivien *et al.*, 2005; La Mesa *et al.*, 2011; Giakoumi & Kokkoris, 2013) and provide a wide array of marine ecosystem services (Salomidi *et al.*, 2012). To assess the ecological status of these habitats, *ad hoc* indices and metrics were applied (Orfanidis *et al.*, 2001; Boudouresque *et al.*, 2006; Montefalcone *et al.*, 2007), along the lines of the Habitats (92/43/EEC) and Water Framework (WFD, 2000/60/EE) EU Directives, taking into account the morphological, structural and life-history features of the habitat-forming macrophytes (macroalgae and *P. oceanica*). Furthermore, an integrated assessment was performed at 5 and 15 m depth, jointly addressing structural aspects of fish assemblages and their associated benthic communities (e.g. Sala *et al.*, 2012).

Fieldwork protocols and data analysis

Ecological status assessment

A. Shallow rocky reefs

The Rapid Assessment of Coastal Ecological Status (RACES) methodology was applied to assess the ecological quality status (*sensu* the WFD) of shallow rocky reefs; this methodology consists in the application of the Ecological Evaluation Index (EEI) (Orfanidis *et al.*, 2001) on photographic samples of macroalgae along the upper infralittoral zone (0-1 m) (Salomidi, 2009). At each site, six systematic randomly placed photoquadrats (21 cm × 30 cm) were obtained at equal distances along a 25 m transect line and the images were analysed at the laboratory. Conspicuous species were identified to the lowest possible taxonomic level or morphological group, and mean percentage cover per species (or higher taxon) was estimated using a superimposed digital grid in the Adobe Photoshop CS5 image editing environment. All taxa identified were assigned to Ecological State Group (ESG) I or II, as defined by their morphological, life-history and ecophysiological traits; the Ecological Evaluation Index (EEI), designed to reflect the macroalgal communities response to varying levels of nutrient enrichment in a water body, was subsequently applied to allow the classification of each site among five distinct Ecological Status categories (i.e. *bad* = 2, *low* = 4, *moderate* = 6, *good* = 8, and *high* = 10) (Orfanidis *et al.*, 2001).

B. *Posidonia oceanica* meadows

To assess the ecological quality status and the vitality of *P. oceanica* meadows, a set of key structural and functional metrics was considered, namely: meadow cover (%), shoot density (shoots m^{-2}), plagiotropic growth of rhizomes (%), and meadow lower limit typology (Appendix, Table 1). Each of these metrics provides useful information on the vitality of the *P. oceanica* meadows for a wide spectrum of anthropogenic disturbances (i.e. nutrient enrichment, sediment resuspension and turbidity, mechanical disturbance) (Pergent-Martini *et al.*, 2005). With the exception of the meadow lower limit typology, all other metrics were sampled at a standard depth of 15 m to prevent the masking effects of depth variability (Alcoverro *et al.*, 1995). Table 1 of the Appendix summarizes all metrics considered along with their anticipated responses to different impacts, and outlines their respective methodological protocols. The interpretation of the estimated values for each metric is based on the standardized scales summarized in Table 2 of the Appendix (Pergent *et al.*, 1995; Boudouresque *et al.*, 2006; Montefalcone, 2009; UNEP/MAP-RAC/SPA, 2011; Pergent *et al.*, 2015).

Integrated assessment of fish and benthic assemblages

A. Infralittoral fish communities

To survey infralittoral fish communities at each site, visual censuses were performed along three replicate 25 m × 5 m transect lines, at 5 m and 15 m depth, where either rocky reefs or *P. oceanica* meadows occurred. The diver conducting the fish survey moved at a constant speed identifying, counting, and attributing all individuals to 5 cm size classes within 2.5 m on either side of the transect lines (La Mesa & Vacchi, 1999). Length estimates of fish counted during the surveys were converted to wet weight by using the allometric length–weight conversion formula: $W = a L^b$, where W is the weight in grams and L is the total length in cm. Parameters a and b are constants obtained from Giakoumi *et al*. (2012) and Fishbase (www.fishbase.org). Where values for a and b were not available, the parameters from congeneric species with similar shape and maximum total length were used. We chose the parameter values that best corresponded

Table 1. Station code name and location, coordinates in decimal degree format (WGS ’84 Datum) and description of the occurring habitat types.

Name	Location	LAT	LON	Depth(m)	Habitat types
AK-1	Akrotiri Peninsula	36.36345	25.39550	5	*Posidonia* bed
				15	Vertical rocky wall
AK-2	Akrotiri Peninsula	36.36774	25.38503	5	*Posidonia* bed
				15	*Posidonia* bed
AK-3	Akrotiri Peninsula	36.36935	25.37799	5	Vertical rocky wall
				15	Vertical rocky wall
AK-4	Akrotiri Peninsula	36.36663	25.36195	5	Horizontal continuous rock
				15	Vertical rocky wall
AK-5	Akrotiri Peninsula	36.35971	25.35969	5	Horizontal continuous rock
				15	*Posidonia* bed
AK-6	Akrotiri Peninsula	36.35665	25.35392	5	Horizontal continuous rock
				15	*Posidonia* bed
AK-7	Akrotiri Peninsula	36.35275	25.36387	5	Vertical wall
				15	*Posidonia* patches on sandy bottom
AN-1	Aspronisi	36.38355	25.35078	5	Horizontal continuous rock with medium boulders
				15	Vertical rocky wall
AN-2	Aspronisi	36.38018	25.34545	5	Horizontal continuous rock with crevices
		36.37772	25.34442	15	*Posidonia* bed
CT-1	Megalochori	36.37400	25.42227	5	Posidonia bed with medium boulders
				15	*Posidonia* bed
CT-2	Akrotiri Peninsula	36.35070	25.37678	5	Medium boulders
				15	*Posidonia* beds
NK-1	Nea Kameni	36.39618	25.40289	5	Large boulders
				15	Large boulders
PK-1	Palia Kameni	36.39310	25.38290	5	Large boulders
				15	Vertical rocky wall
PK-2	Palia Kameni	36.39746	25.37473	5	Large boulders
				15	Large boulders
PR-1	Perissa Rock	36.36563	25.48410	5	Sub-horizontal wall
PR-2	Perissa Rock	36.36232	25.48697	5	Vertical rocky wall
		36.36157	25.48739	15	Sandy with *Posidonia* patches
PR-3	Perissa Rock	36.36038	25.48563	7-9	Horizontal continuous rock with small boulders
PR-4	Perissa Rock	36.35883	25.48294	5	Vertical rocky wall
		36.35601	25.48396	15	Sandy with large *Posidonia* patches

Table 2. Vitality of *Posidonia oceanica* meadows. Mean values (± SE) of each metric per sampling site.

Sampling Site	Lower Limit type	Meadow Cover (%)	Conservation Index (CI)	Shoot density (shoots m^{-2})	Plagiotropic growth of rhizomes (%)	Synthesis (Mean metric values)
AK-2	Erosive	92.0 ± 6.1	0.97 ± 0.01	289.6 ± 41.3	27.2 ± 6.8	4.0 (*good*)
AK-5	Erosive	55.3 ± 5.9	0.82 ± 0.38	514.6 ± 33.1	12.0 ± 2.1	4.2 (*good*)
AK-6	Progressive	68.4 ± 6.2	0.81 ± 0.11	418.7 ± 19.9	15.5 ± 3.4	4.0 (*good*)
AN-2	Progressive	64.8 ± 5.1	0.94 ± 0.03	637.5 ± 40.3	12.7 ± 2.5	4.5 (*good*)
CT-1	Erosive	95.6 ± 4.4	0.96 ± 0.04	310.4 ± 43.6	11.8 ± 4.5	4.0 (*good*)
CT-2	Progressive	71.3 ± 3.2	0.93 ± 0.04	581.3 ± 30.3	12.3 ± 1.1	4.5 (*good*)
PR-2	Progressive	71.2 ± 3.3	0.93 ± 0.04	364.6 ± 29.7	27.3 ± 7.0	4.0 (*good*)
PR-4	Progressive	41.2 ± 12.5	0.86 ± 0.08	404.3 ± 67.1	34.5 ± 8.7	3.7 (*good*)

to our study area (Cyclades Islands), or the closest geographical area available (usually located in the Eastern Mediterranean). Fish taxa were assigned to functional groups based on published diet and trophic level data (www.fishbase.org), i.e. zooplanktivores, herbivores, carnivores and apex predators (Guidetti & Sala, 2007; Giakoumi & Kokkoris, 2013).

B. Structure and composition of benthic communities

The composition and structure of benthic communities were studied within 12 replicate quadrats (20 cm × 20 cm) randomly placed along each 5 m and 15 m transect line, provided that rocky substrata occurred at these depths. For each quadrat, the percentage cover (%) of the different benthic components was estimated *in situ*, and classified into distinct layers (Sala *et al*., 2012), namely the canopy (large-sized perennial slow-growing algae, i.e. *Cystoseira*, *Sargassum*), the bushy (fleshy medium-sized algae that typically occupy the open space between and underneath the canopy, e.g. *Padina, Dictyota, Halopteris, Gelidium*), the calcified (including both erect, e.g. *Amphiroa, Jania*, and encrusting corallines, e.g. *Lithophyllum, Mesophyllum*), the turf (consisting of minute, typically seasonal and fast growing species, e.g. *Sphacelaria, Cladophora, Bryopsis,* also including cyanophyte and chrysophyte mats), and the epiphyte layer (comprising minute seasonal species, e.g. *Ceramium, Dasya, Herposiphonia*, growing on larger algal thalli). Benthic invertebrates and bare rock, identified as rocky substratum deprived of any marine macrobiota, were also recorded and treated as separate layers in the analyses.

C. Sea urchin biomass

Sea urchin size and density were recorded using 50 cm × 50 cm quadrat frames placed randomly along the 5 m and 15 m transect lines. A total of 12 quadrats (4 per transect), i.e. an area of 3 m^2 were sampled per depth at each site. The size of each individual (>1 cm test diameter without spines) was measured *in situ* using calipers. Sea urchins were grouped into 1 cm size classes (Sala & Zabala, 1996) in order to examine the size-frequency distribution of their populations. Biomass was estimated based on the size-weight relationships provided by a previous study conducted in the same region (Giakoumi *et al*., 2012).

Other species of interest

At all sites and transect lines surveyed, the presence of conspicuous species, with special emphasis on species of conservation interest and alien species, was recorded *in situ* upon detection. For the list of benthic invertebrates of special conservation interest, all relevant national laws and Annexes of the EU directives and international agreements were considered, namely the Greek Presidential Decrees 67/1981; 227/200; 109/2002; The Red List of IUCN; The Red Book of Threatened Animals of Greece, 2009; Habitats Directive 92/43/EEC; The Bern Convention, 1979; The Protocol of Barcelona Convention, 1995; and the CITES Convention, 1973.

Statistical Analyses

Differences between sampling sites were tested using One-way ANOVA for independent samples when conditions of normality and homogeneity of distribution were met; if not, the non-parametric Kruskal-Wallis H-test was applied. Normality of distribution was investigated using the Shapiro-Wilk normality test and homogeneity of variance using Levene's test. Correlations among variables were tested using Spearman's rank correlation coefficient. All differences were considered significant at $p < 0.05$. Similarity percentage analysis (SIMPER) was performed to detect and express dissimilarities in benthic community layers between stations using the unprocessed algal data set.

Data analyses were performed using the IBM SSPS Statistics 20, STATISTICA StatSoft™ v.6, R Core Team (2016), and PRIMER v.6.1.8 software packages.

Results

Of all sites inspected, continuous horizontal rocky substratum was the most widespread habitat type at both survey depths, i.e. 5 m and 15 m (Table 1). *P. oceanica* meadows were also common, especially at 15 m depth. Sandy bottoms, gravel and boulders were ubiquitous across the study area, while coralligenous assemblages, drop-offs and overhangs were particularly common along the steep-sloping Caldera coasts.

Ecological status assessment

A. Shallow rocky reefs

Out of a total of 108 photoquadrat samples, 19 phytobenthic taxa were identified, among which 7 down to species level, 6 to genus level and the rest within higher taxonomic or morphological groups (e.g. *Laurencia* spp. complex, filamentous turf, encrusting red algae). Thick leathery perennial species of *Cystoseira* were dominant almost throughout the upper infralittoral zone of the study area (mean cover ± SE: 42.8 ± 4.8%), followed by turf algae (including various filamentous opportunistic families, e.g. Cladophorales, Ceramiales, Sphacelariales) (20 ± 2.8%), erect calcified species of *Jania* (18.8 ± 2.3%), and various encrusting red algae such as the crustose perennial *Lithophyllum* spp. (6.9 ± 1.6%). The alien *Caulerpa cylindracea* was only detected in low cover (0.1 ± 0.09%). A list of all taxa identified, their mean cover values ± SE across sites and their respective ESG category, is given in Table 3 of the Appendix.

According to the SIMPER analysis, most sites presented a high level of similarity (71.4%) for which *Cystoseira* spp., *Jania* spp. and turf algae were identified as the main contributing taxa (55.3%, 20.5% and 17.3% respectively). Only stations NK-1 (Nea Kameni Islet) and PR-1 (Perissa Rock, north) showed significant dissimilarity (*Kruskal-Wallis test*, $p < 0.005$), mostly due to the scarcity of *Cystoseira* spp. (contributing by 34.9%) and the relatively increased local dominance of the *Laurencia* species complex, turf algae, *Sargassum* spp., and *Jania* spp. (contributing 19.5%, 13.9%, 12.9%, and 10.4% respectively).

The application of the EEI index classified most sites within *good* or *high* ecological status, but stations AK2 and AK6 were evaluated as *moderate*, and station NK-1 as *bad* (Fig. 2). The mean EEI numerical value calculated for the whole study area was 8.8 ± 2.18, reaching up to 9.2 ± 1.42 if the highly disturbed NK-1 station is excluded. These values correspond to a *good* to *high* ecological status largely characterizing the upper infralittoral rocky shores (83.3% of the studied stations), both within and outside the sheltered Caldera region.

B. *Posidonia oceanica* meadows

Given the steep topography (i.e. sudden drop-offs) and the wide prevalence of rocky substrata, the distribution of *P. oceanica* meadows in the study area appeared to be primarily driven by geomorphology. *P. oceanica* meadows were naturally restricted to depths between 5 m and 22 m and presented a rather patchy distribution. The only exception was the relatively shallow underwater ridge connecting Akrotiri Cape to Aspronisi Island, where milder slopes enabled the development of more extensive and slightly deeper meadows (maximum depth of 25 m).

Overall, 8 suitable sampling sites (i.e. extensive meadows at 15 m depth) were selected within the wider study area. Mean values (± SE) of each metric as estimated per site are summarized in Table 2. All meadows studied were dense (shoot density = 461 ± 45.11 shoots m^{-2}) and presented a *good* conservation status (Conservation Index, CI = 0.89 ± 0.02). Their overall vitality was invariably evaluated as *good* (Table 2).

Data analysis indicated statistically significant differences among stations for all metrics (meadow cover: $H = 7.626, p < 0.001$; shoot density: $F = 10.389, p < 0.001$; plagiotropic growth of rhizomes: $H = 15.753, p = 0.027$), except for the CI ($H = 7.095, p = 0.419$) (Fig. 3). *Post-hoc* analysis revealed a possible differentiation pattern for the stations, based on their spatial distribution, only as regards shoot density and percentage of plagiotropic growth of rhizomes (Fig. 3). More specifically, highest shoot density and lowest percentages of plagiotropic growth of rhizomes were detected at sites located along the southern coasts of Akrotiri Peninsula (Table 2; Fig. 3).

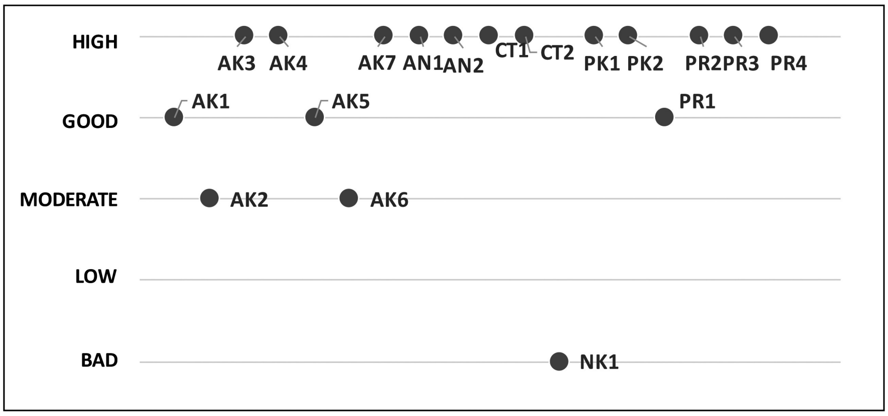

Fig. 2: Ecological status categories as determined per site according to the Ecological Evaluation Index.

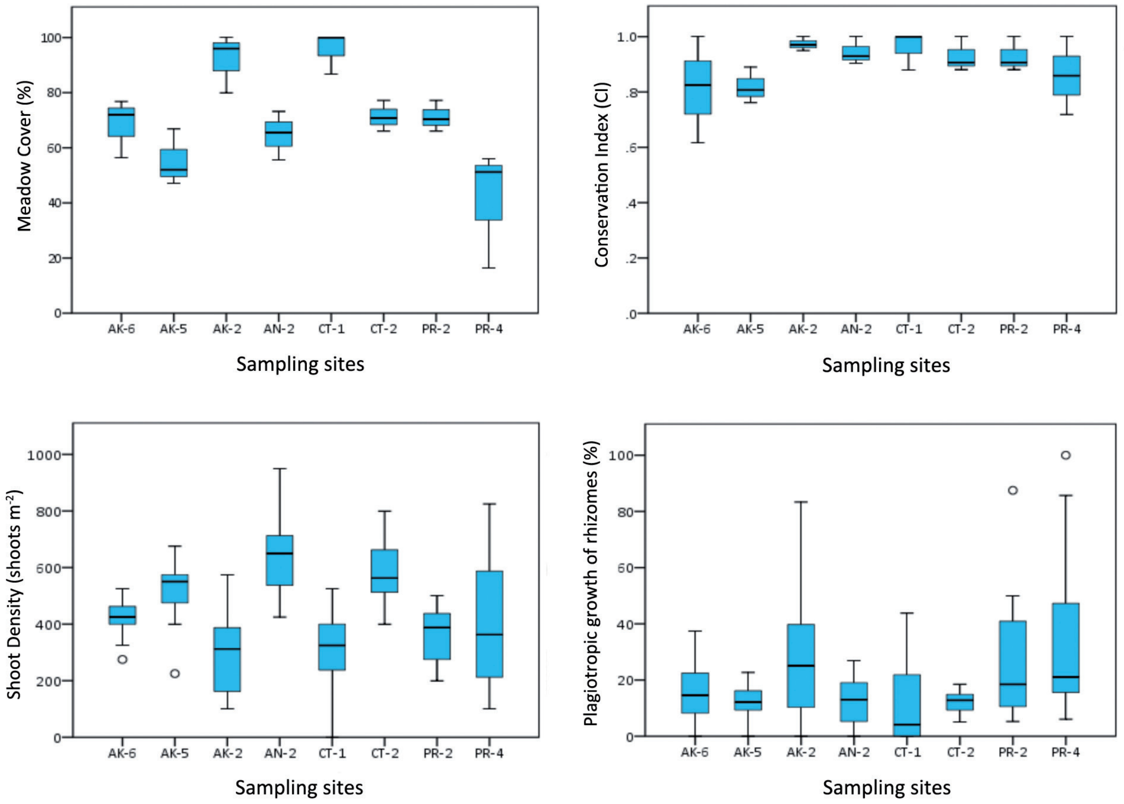

Fig. 3: Boxplots depicting spatial variability of *Posidonia oceanica* metrics among the studied sites. Boxes and whiskers represent within site variability.

Integrated assessment of fish and benthic assemblages

A. Infralittoral fish communities

We counted and estimated the length of 14,659 fish specimens belonging to 38 species and 16 families. Another 5 families (Mugilidae, Atherinidae, Blennidae, Gobiidae and Tripterygiidae) were recorded but not identified to species level. The most abundant family was the Pomacentridae consisting of the single species *Chromis chromis*, while the families with most species were the Labridae (9 species) and the Sparidae (8 species). The vast majority of fish encountered (81% at 5 m depth and 68% at 15 m depth) belonged to 0-5 and 5-10 cm size classes. Accordingly, most individuals of commercially exploited species recorded were juveniles (Fig. S1–S8). At 5 m depth, total fish biomass presented a mean value (± SE) of 7.96 ± 2.14 g m^{-2} across rocky sites, and 11.4 ± 4.35 g m^{-2} across sites with *P. oceanica* meadows (Fig. 4A). At 15 m depth, the mean value of total biomass was 10.6 ± 2.41 g m^{-2} across rocky sites, and 12.7 ± 2.79 g m^{-2} across sites with *P. oceanica* meadows (Fig. 4D). Total biomass between 5 m and 15 m did not differ significantly (*Kruskal-Wallis test, p > 0.05*). However, the biomass corresponding to the different trophic groups differed between the two depths (Table 3). At 5 m depth, herbivores accounted for the largest proportion of total biomass at most sites, whereas at 15 m depth zooplanktivores were the predominant trophic group. At both depths, apex predators represented a very small proportion – as only few small-sized individuals were encountered (Fig. S5) – and were totally absent at half of the sampling sites. Three alien fish species, all of Red Sea origin, were recorded during the visual surveys: the dusky spinefoot *Siganus luridus,* the marbled spinefoot *Siganus rivulatus*, and the bluespotted cornet fish *Fistularia commersonii*. At 5 m depth, the siganids accounted for 82% of herbivorous fish biomass and 44% of total fish biomass. At 15 m depth, the siganids accounted for 74% of herbivorous fish biomass and 14% of total fish biomass. Most siganids encountered belonged to the 10-15 cm size class (Fig. S9 and S10).

B. Structure and composition of benthic communities

Rocky infralittoral sites at 5 m depth exhibited benthic communities mainly dominated by turf algae (mean cover ± SE: 61.4 ± 19.6%), followed by calcified algae (14.7 ± 11.4%). Bare rock was also found to be common within quadrats with a mean cover of 9 ± 7.3%. On the

Table 3. Results of Kruskal-Wallis test on differences in fish group biomass between sites at 5 m and 15 m depth.

Fish group	Chi-squared	df	p-value
Zooplanktivores	6.52	1	0.010
Herbivores	7.6237	1	0.005
Carnivores	1.9048	1	0.167
Apex predators	3.5363	1	0.060

other hand, the canopy layer, which usually characterizes pristine Mediterranean shores, was found to be greatly reduced (6.7 ± 7.9%), consisting of only a few *Cystoseira* species (mainly *C. spinosa*, but also *C. corniculata, C. elegans and C. foeniculacea* f. *tenuiramosa*). The bushy layer (including *Padina pavonica, Halopteris scoparia, Codium bursa, Dictyopteris polypodioides, Gelidium bipectinatum*) was also poor, with a mean cover not exceeding 6.3 ± 9.4%, while the respective values for epiphytes and invertebrates (mainly sponges and bivalves) (Fig. 4C) were even lower (<2%). The benthic structure and composition at 15 m depth, where turf algae were also dominant (62.1 ± 16.2%) (Fig. 4F), followed by calcified algae and bare rock (12.7 ± 8.1% and 10.5 ± 5.5% respectively) was quite similar. Again, the canopy and bushy layers were poor (5.5 ± 8.1% and 7.6 ± 4.4% respectively), while invertebrates and epiphytes presented low values (<1.3%). Overall, no statistically significant differences were observed between the cover of benthic communities at 5 m and 15 m depth (*Kruskal-Wallis test, p > 0.05*).

C. Sea urchin biomass

Two species of sea urchin were encountered, namely *Paracentrotus lividus* and *Arbacia lixula*. The density and biomass of sea urchins were found to be very low at both depths. At 5 m depth, sea urchins were recorded at half of the studied sites (Fig. 4B), with total biomass ranging between 13.6 and 267.6 gr m^{-2}, and a mean value (± SE) of 61.6 ± 26.8 gr m^{-2}. At 15 m depth, only few juvenile sea urchins (<2 cm) of the species *A. lixula* were recorded at only one station where total biomass was 8.07 gr m^{-2} (Fig. 4E).

D. Relationships between fish and benthic assemblages

No significant relationships were detected between total fish biomass or fish carnivore biomass and sea urchin biomass across sites. Furthermore, no significant relationship was detected between sea urchin and *Diplodus* spp. biomass, which are the main predators of adult sea urchins. At 5 m depth, a positive relationship between herbivore fish and bare rock ($r_s = 0.563, p = 0.02$) was revealed, whereas negative relationships were detected between canopy algae and herbivorous fish ($r_s = -0.486, p = 0.05$), as well as with sea urchins ($r_s = -0.505, p = 0.04$).

Other species of interest

A total of 92 macrobenthic invertebrate species were recorded throughout our study area belonging to 9 higher taxa (Table 4). The list includes 12 species that are protected by international regulations and conventions, 11 species of commercial interest whose harvesting is regulated by national regulations and international laws, and two alien species.

Conspicuous benthic invertebrates that were consistently recorded throughout the entire study area were the sponges *Crambe crambe, Spirastrella cunctatrix*, *Agelas oroides*, *Petrosia ficiformis*, *Chondrosia reniformis* and *Sarcotragus foetidus*, the bryozoans *Schizoporella* cf. *dunkeri* and *Reptadeonella violacea*, the nudibranch *Peltodoris atromaculata* (always associated with *P. ficiformis* sponges), the ascidian *Halocynthia papillosa* and the bivalve *Spondylus gaederopus*. Other relatively common species of conservation interest were the bivalve *Pinna nobilis*, sponges of the genus *Axinella* (mainly *A. polypoides*), the brown cowry (*Luria lurida*) and the scleractinians *Balanophyllia europaea* and *Madracis pharensis*. The finding of several dead shells of Triton's trumpet (*Charonia variegata*) also indicates the presence of this otherwise elusive – due to its mostly nocturnal habits – protected species. With regard to alien invertebrates, only the sub-tropical crab *Percnon gibbesi* was commonly encountered, exclusively at stations within the Caldera. The bivalve *Pinctada imbricata radiata* was found at only one site of the Perissa Rock, while a couple of dead shells of the gastropod *Conomurex persicus* suggest potential presence of live specimens as well.

A comprehensive inventory of all species recorded at each site (0-1 m, 5 m and 15 m observations integrated) is given in Table 5.

Discussion

Good environmental quality conditions were found to characterize the upper infralittoral rocks of southern Santorini Island, as reflected in rich late successional algal communities dominated by *Cystoseira* species. Both sheltered and exposed shallow rocky coasts along Akrotiri Peninsula, Perissa Rock and the islets of Caldera were assessed as presenting a *good* to *high* ecological status according to the EEI scale. Few exceptions were detected, among which the striking case of the southern coast of Nea Kameni Islet where few *r-selected* species (mainly turf algae and species of the *Laurencia* complex) practically monopolized the rocky substratum, a sharp contrast to the lavish algal communities that once thrived here under the effect of volcanic seeps (authors' personal observations, 2007).

Table 4. Number of benthic invertebrate species recorded across sites (Total, Protected, Commercially Important and Alien).

Higher taxa	**Total Number**	**Protected**	**Commercial**	**Alien**
Foraminifera	1			
Porifera	27	4		
Cnidaria	8	4		
Annelida	4			
Mollusca	23	3	9	2
Crustacea	2			1
Bryozoa	7			
Echinodermata	12	1	1	
Tunicata	8		1	
Sum	**92**	**12**	**11**	**3**

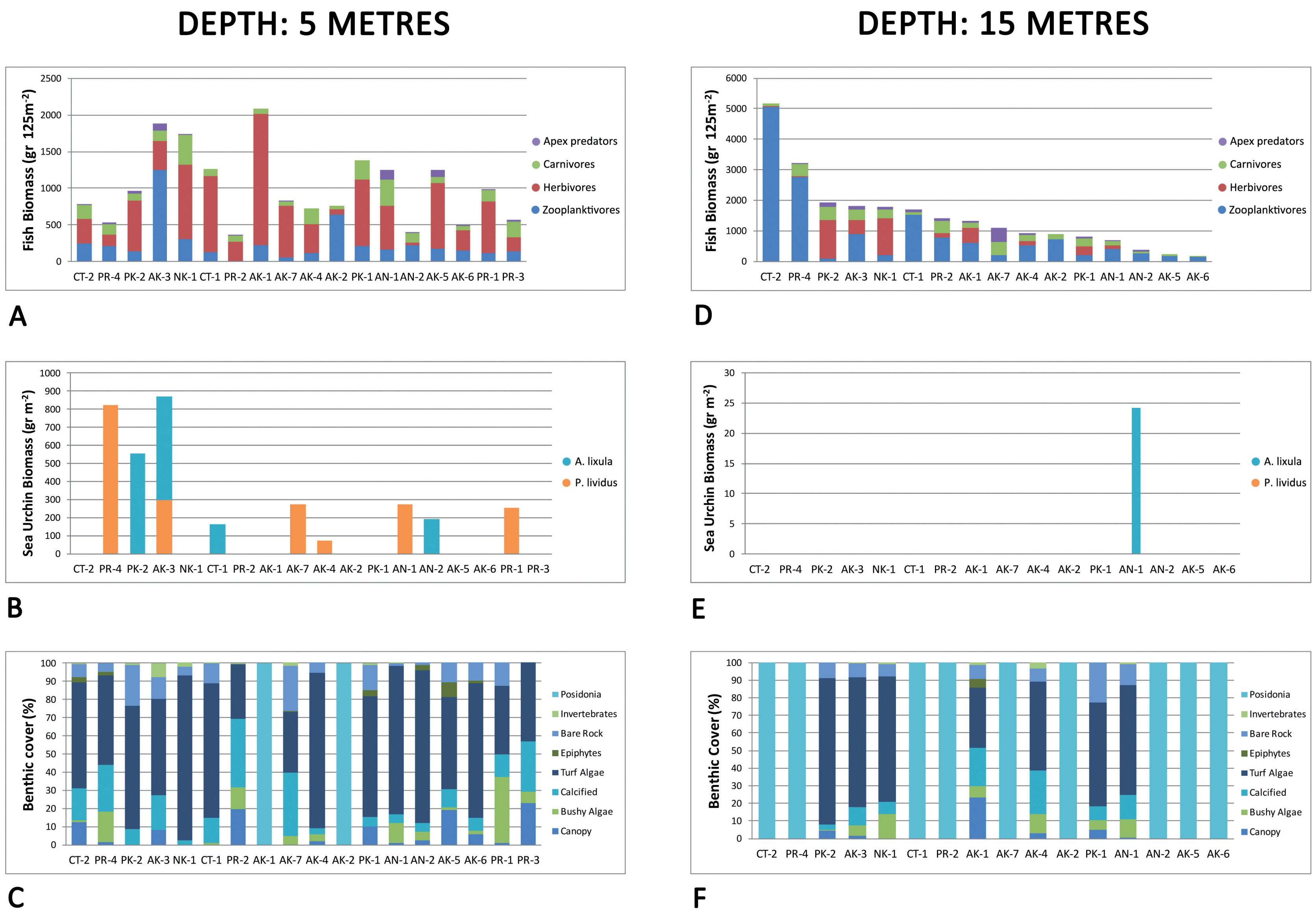

Fig. 4: Panel of bar-charts demonstrating the following per site: the distribution of mean fish biomass among trophic groups (apex predators, carnivores, herbivores, zooplanktivores) at A) 5 m and D) 15 m; the mean sea urchin (*Paracentrotus lividus* and *Arbacia lixula*) biomass at B) 5 m and E) 15 m; and the mean percentage cover of benthic layers: *Posidonia oceanica*, invertebrates, bare rock, epiphytes, turf algae, calcified algae, bushy algae and canopy algae at C) 5 m and F) 15 m respectively.

Table 5. Presence of invertebrate species recorded per site (all studied depths summarized), and their respective information on conservation or other interest. “Status” details are given below.

				Perissa Rock Sites				Akrotiri Peninsula							Control Sites						
Phylum	**Species**	**Authority**	**Status**	**PR1**	**PR2**	**PR3**	**PR4**	**AK1**	**AK2**	**AK3**	**AK4**	**AK5**	**AK6**	**AK7**	**CT1**	**CT2**	**PK1**	**PK2**	**NK1**	**AN1**	**AN2**
FORAMINIFERA																					
Foraminifera	*Miniacina miniacea*	Pallas, 1766							+			+									+
PORIFERA																					
Porifera	*Acanthella acuta*	Schmidt, 1862						+		+	+						+	+		+	+
Porifera	*Agelas oroides*	Schmidt, 1864		+		+		+	+	+	+		+	+		+	+	+	+	+	
Porifera	*Aplysina aerophoba*	Nardo, 1833	1/II					+		+	+	+			+					+	
Porifera	*Axinella cannabina*	Esper, 1794	1/II								+									+	
Porifera	*Axinella damicornis*	Esper, 1794								+	+			+						+	
Porifera	*Axinella polypoides*	Schmidt, 1862	1/II; 2/II					+	+		+			+			+	+		+	
Porifera	*Axinella verucosa*	Esper, 1794																		+	
Porifera	*Calyx nicaeensis*	Risso, 1826									+				+				+	+	
Porifera	*Chondrilla nucula*	Schmidt, 1862									+				+				+	+	+
Porifera	*Chondrosia reniformis*	Nardo, 1847		+	+	+	+			+	+	+	+				+	+	+	+	+
Porifera	*Cliona* sp.					+												+			
Porifera	*Cliona celata*	Grant, 1826						+			+										
Porifera	*Cliona* cf. *parenzani*	Corriero & Scalera-Liaci, 1997		+																	
Porifera	*Cliona viridis*	Schmidt, 1862							+								+		+	+	
Porifera	*Crambe crambe*	Schmidt, 1862			+	+		+		+	+	+			+		+	+	+	+	
Porifera	*Dictyonella incisa*	Schmidt, 1880									+						+		+	+	
Porifera	*Haliclona* sp.								+												
Porifera	*Hemimycale columella*	Bowerbank, 1874									+					+					
Porifera	*Ircinia* spp.									+	+								+	+	
Porifera	*Ircinia oros*	Schmidt, 1864								+	+									+	
Porifera	*Ircinia variabilis*	Schmidt, 1862									+						+			+	
Porifera	*Petrosia ficiformis*	Poiret, 1789		+	+		+	+	+	+	+	+		+		+	+	+	+	+	
Porifera	*Phorbas fictitius*	Bowerbank, 1866		+		+				+	+					+					+
Porifera	*Phorbas tenacior*	Topsent, 1925																	+		
Porifera	Porifera unid.													+		+	+	+	+	+	
Porifera	*Sarcotragus foetidus*	Schmidt, 1862	1/II	+	+		+			+	+	+	+	+		+		+	+		
Porifera	*Scalarispongia scalaris*	Schmidt, 1862		+														+			
Porifera	*Spirastrella cunctatrix*	Schmidt, 1868		+		+	+			+	+	+	+	+	+	+	+	+	+	+	+
CNIDARIA																					
Cnidaria	*Anemonia viridis*	Forskål, 1775							+			+									
Cnidaria	*Balanophyllia europaea*	Risso, 1826	4/II; 5/DD									+	+			+	+	+	+		
Cnidaria	*Cerianthus membranaceous*	Spallanzani, 1784					+	+													
Cnidaria	*Condylactis aurantiaca*	Delle Chiaje, 1825				+						+									

(continued)

Table 5 *(continued)*

Phylum	Species	Authority	Status	Perissa Rock Sites				Akrotiri Peninsula							Control Sites						
				PR1	PR2	PR3	PR4	AK1	AK2	AK3	AK4	AK5	AK6	AK7	CT1	CT2	PK1	PK2	NK1	AN1	AN2
Cnidaria	*Eudendrium* spp.							+		+											
Cnidaria	*Leptopsammia pruvoti*	Lacaze-Duthiers, 1897	4/II					+			+									+	
Cnidaria	*Madracis pharensis*	Heller, 1868	4/II; 5/LC		+						+			+			+	+	+	+	
Cnidaria	*Polycyathus muellerae*	Abel, 1959	4/II								+			+							
Cnidaria	Scleractinia unid.																		+		
ANNELIDA																					
Annelida	*Hermodice carunculata*	Pallas, 1766		+			+		+				+						+		+
Annelida	*Protula* sp.																+				
Annelida	*Sabella spallanzanii*	Gmelin, 1791						+		+											
Annelida	*Serpulidae* spp.			+		+		+		+		+					+	+	+	+	
MOLLUSCA																					
Mollusca	*Bittium* sp.																+				
Mollusca	*Bolma rugosa*	Linnaeus, 1767	9					+	+								+	+	+		
Mollusca	*Cerithium* sp.					+					+										
Mollusca	*Hexaplex trunculus*	Linnaeus, 1758																	+	+	
Mollusca	*Elysia timida*	Risso, 1818								+							+				
Mollusca	*Felimare picta*	Schultz in Philippi, 1836							+												
Mollusca	*Luria lurida*	Linnaeus, 1758	1/II; 2/II; 6; 9							+	+				+		+				
Mollusca	*Octopus vulgaris*	Cuvier, 1797	9	+																+	+
Mollusca	*Pecten* sp.																				+
Mollusca	*Peltodoris atromaculata*	Bergh, 1880		+			+	+	+	+	+			+			+	+	+	+	
Mollusca	*Pinctada imbricata radiata*	Leach, 1814	9;10		+																
Mollusca	*Pinna nobilis*	Linnaeus, 1758	1/II; 2/II; 3/ IV; 6;7;8;9				+		+						+						
Mollusca	*Pinna rudis*	Linnaeus, 1758							+			+	+						+		+
Mollusca	*Sepia officinalis*	Linnaeus, 1758	9																	+	
Mollusca	*Thylacodes arenarius*	Linnaeus, 1758				+										+		+			+
Mollusca	*Spondylus gaederopus*	Linnaeus, 1758	7;8;9	+	+		+	+		+			+				+	+	+	+	+
Mollusca	*Thuridilla hopei*	Vérany, 1853			+																
Mollusca	*Umbraculum umbraculum*	Lightfoot, 1786																		+	
Mollusca	*Vermetidae* spp.	(Roth) C.Agardh, 1823									+	+			+		+	+	+	+	
CRUSTACEA																					
Crustacea	*Paguridae* spp.					+	+				+		+				+	+	+	+	
Crustacea	*Percnon gibbesi*	H. Milne-Edwards, 1853	10										+		+			+			
BRYOZOA																					
Bryozoa	Bryozoa unid.							+													
Bryozoa	*Margaretta cereoides*	Ellis & Solander, 1786							+			+		+	+						+
Bryozoa	*Myriapora truncata*	Pallas, 1766								+							+	+	+	+	

(continued)

Table 5 *(continued)*

				Perissa Rock Sites				Akrotiri Peninsula							Control Sites						
Phylum	**Species**	**Authority**	**Status**	**PR1**	**PR2**	**PR3**	**PR4**	**AK1**	**AK2**	**AK3**	**AK4**	**AK5**	**AK6**	**AK7**	**CT1**	**CT2**	**PK1**	**PK2**	**NK1**	**AN1**	**AN2**
Bryozoa	*Reptadeonella violacea*	Johnston, 1847			+	+				+	+	+	+	+	+	+	+	+	+	+	+
Bryozoa	*Rhynchozoon neapolitanum*	Gautier, 1962			+	+					+						+				
Bryozoa	*Schizomavella mamillata*	Hincks, 1880			+									+							
Bryozoa	*Sertella* sp.								+			+									+
Bryozoa	*Schizoporella cf. dunkeri*	Reuss, 1848			+	+				+	+	+	+	+	+	+	+	+	+	+	+
ECHINODERMATA																					
Echinodermata	*Amphiura filiformis*	O.F. Müller, 1776																+	+		
Echinodermata	*Arbacia lixula*	Linnaeus, 1758		+				+					+		+						
Echinodermata	*Coscinasterias tenuispina*	Lamarck, 1816															+				+
Echinodermata	*Echinaster sepositus*	Retzius, 1783						+													
Echinodermata	*Hacelia attenuata*	Gray, 1840																	+		
Echinodermata	*Holothuridae unid.*									+											
Echinodermata	*Holothuria forskali*	Delle Chiaje, 1823					+														
Echinodermata	*Holothuria sanctori*	Delle Chiaje, 1824															+				
Echinodermata	*Marthasterias glacialis*	Linnaeus, 1758																	+		
Echinodermata	*Ophidiaster ophidianus*	Lamarck, 1816	1/II; 2/II				+			+											
Echinodermata	*Paracentrotus lividus*	Lamarck, 1816	9	+						+	+	+		+							
Echinodermata	*Sphaerechinus granularis*	Linnaeus, 1758																	+		
TUNICATA																					
Tunicata	*Aplidium elegans*	(Giard, 1872)															+				
Tunicata	*Clavelina* sp.										+										
Tunicata	*Didemnidae* spp.			+																	
Tunicata	*Didemnum maculosum*	(Milne-Edwards, 1841)													+						
Tunicata	*Diplosoma spongiforme*	Giard, 1872															+				
Tunicata	*Microcosmus* spp.																+				
Tunicata	*Microcosmus sabatieri*	Roule, 1885	9															+	+	+	
Tunicata	*Polysyncraton lacazei*	Giard, 1872																			+
DEAD SHELLS																					
Mollusca	*Conomurex persicus*	Swainson, 1821	10														+				
Mollusca	*Luria lurida*	Linnaeus, 1758	1/II; 2/II; 6; 9															+			+
Mollusca	*Ostrea* sp.		6; 9																+		
Mollusca	*Spondylus gaederopus*	Linnaeus, 1758	7; 8; 9								+						+		+		
Mollusca	*Semicassis granulata*	Born, 1778				+															
Mollusca	*Charonia tritonis variegata*	Lamarck, 1816	1/II; 2/II; 9						+						+						+

1. Barcelona Convention - Protocol concerning Specially Protected Areas and Biological Diversity in the Mediterranean; **2. Bern Convention** - Convention on the conservation of European wildlife and natural habitats; **3. Habitats Directive 92/43/EEC**; **4. CITES** - Convention on International Trade in Endangered Species of Wild Fauna and Flora, 1973; **5. Red List of IUCN** - the International Union of Conservation of Nature; **6.** Presidential Decree 67/1981; **7.** Presidential Decree 109/2002; **8.** Presidential Decree 227/200; **9.** Exploited Species; **10.** Alien (non indigenous) species; **I, II, III, IV.** Appendix/Annex I, II, III, IV, **DD.** Data deficient; **LC.** Least Concern

These exceptions, however, are not clearly associated with coastal sources of nutrient enrichment and likely reflect strictly localized or seasonal stresses that should be regarded as outliers to an otherwise healthy ecosystem component.

Similarly, healthy ecological conditions were reflected in the adjacent *P. oceanica* meadows, which have been studied for the first time so thoroughly in the Cyclades Archipelago. Critical evaluation of the applied set of metrics revealed that the meadows of Santorini are still in equilibrium and present a good vitality status. Slight deviations from reference conditions were detected, such as the comparatively lower shoot densities recorded at a few sites along the Akrotiri Peninsula, which may be related to more intense pressures exerted here by recreational activities, i.e. boat anchoring and mooring. Even in these cases, however, meadows were observed to respond positively through increased plagiotropic rhizome growth (Francour *et al*., 1999).

Both evaluation approaches described above, are in agreement with the *high* ecological status that has been assessed through the application of the BENTIX biotic index on soft bottom zoobenthic communities of previous monitoring studies conducted in Santorini Caldera (HCMR, 2011; 2012) that adequately express an oligotrophic area, largely unaffected by either organic or inorganic pollutants (HCMR, 2007-2012).

However, the case of fish and rocky infralittoral benthic communities is more alarming. Notably, fish biomass displayed very low values in the study area as compared to other parts of the Mediterranean, a result that is consistent with a previous study in the wider Cyclades region (Giakoumi *et al*., 2012). Apex predators, in particular, were encountered in low numbers and small sizes at most sites, or were totally absent at several others. In contrast, pristine areas and well-enforced marine reserves are characterised by a dominance of top predators in terms of total fish biomass, presenting an inverted (top-heavy) biomass pyramid (DeMartini *et al*., 2008; Sandin *et al*., 2008). In such pristine habitats, an increase in total fish biomass has been documented, mostly characterised by a greater increase in apex predator biomass (Sandin *et al*., 2008). In that light, the low apex predator biomass that was invariably recorded in the study area, indicates a depleted coastal fish community.

This conclusion is further supported by the fact that the vast majority of commercially exploitable specimens encountered were juveniles (Fig. S1-S8).

The predominant presence of two invasive herbivore fishes, i.e. *S. luridus* and *S. rivulatus*, was remarkable. During the study period (October 2012), large schools of these species thrived in the waters of Santorini, whereas during field surveys conducted in July 2008 only *S. luridus* had been recorded (Giakoumi, 2014). This recent introduction of *S. rivulatus* must have increased grazing pressure in the area. Both these lessepsian species are capable of significantly altering the structure and composition of the infralittoral marine vegetation in the Mediterranean (Sala *et al*., 2011; Giakoumi, 2014), and thus their overabundant populations in the study area pose a direct threat to its native algal communities.

Indeed, the infralittoral vegetation at both 5 m and 15 m depth was mainly characterized by turf algae, various calcified species and the ubiquitous presence of bare rock. On the contrary, the perennial canopy algae of the order Fucales – widely recognized as the main component of the shallow pristine Aegean (e.g. Montesanto & Panayotidis, 2001) and Caldera rocky coasts in particular (HCMR, 2007; 2008) – were only barely recorded during this study. Likewise, the cover of bushy algae, epiphytes and benthic invertebrates was low.

This type of phycocommunity seems to reflect the effects of fish overgrazing (Sala *et al*., 2011), to which turf algae are able to resist by virtue of their decumbent forms, rapid development and short life cycles, while calcified algae by virtue of their hard and rigid thalli. Canopy and bushy algae, on the other hand, are particularly prone to fish overgrazing since their palatable massive fronds readily attract herbivorous species. These observations were confirmed by the statistically significant negative relationship observed between herbivore fishes and canopy algae, and the positive relationship of herbivorous fishes and bare rock. Furthermore, the persistent dominance of canopy algae (*Cystoseira* spp. and, to a lesser degree, *Sargassum* sp.) in the upper infralittoral zone (0-1 m) is yet another indication that their scarcity in deeper habitats is a result of overgrazing; indeed, the upper infralittoral communities are too exposed to water movement and other risks (e.g. seabird predation) for most fish to use as safe foraging grounds.

Sea urchins have been traditionally regarded as keystone grazers influencing the structure and distribution of Mediterranean infralittoral macroalgal communities (e.g. Sala *et al*., 1998; Bulleri *et al*., 1999). When present in high densities, sea urchin grazing pressure may lead to complete depletion of macroalgal forests and the creation of extensive barren rocks mostly dominated by encrusting red algae (Sala *et al*., 1998; Guidetti & Sala, 2007). In our study area, sea urchin abundance and biomass were found to be particularly low compared to other areas of the Cyclades Islands and the Mediterranean Sea (Giakoumi *et al*., 2012, and references therein). In fact, most of the individuals recorded were juveniles. However, a statistically significant negative relationship was found between sea urchin biomass and canopy algal cover. Thus, while it is likely that herbivorous fishes are protagonists in forming the marine vegetation along the coasts of Santorini Island, synergistic effects from sea urchin grazing may still occur.

Most coastal sites studied along Perissa Rock, Akrotiri Peninsula and the adjacent islets were found to comprise a rich variety of habitats and benthic invertebrates, especially within the volcanic caldera, where the much steeper and more complex topography (Nomikou *et al*., 2014) accounted for higher heterogeneity at relatively small scales.

Besides the great number of siganids and their overgrazing effects, other alien species recorded (i.e. the green alga *C. cylindracea*, the red alga *Ganonema farinosum*, the crab *P. gibbesi*, and the trumpet fish *F. commersoni*) were only occasional findings. However, on the positive side, the persistent brown algae canopies on the upper infralittoral rocky shores, as well as the presence of several juveniles of the apex predator *Epinephelus marginatus* suggest the area's potential for ecosystem recovery once a fully protected area is established and appropriate management measures are implemented.

Overall, notwithstanding minor variations among sites, our study area was assessed as undisturbed by anthropogenic pollution, but highly disturbed by the combined pressures of long-term overfishing and excess herbivory by the increasing populations of invasive fish species. The establishment of an MPA is likely to enhance ecosystem recovery by stimulating the recovery of the functional role of top predators, and especially large groupers, which are known to prey on siganids in the Eastern Mediterranean (Aronov & Goren, 2008). Given, however, the strong alterations in ecosystem structure, the establishment of the MPA will have to be accompanied by early restoration actions targeting the decrease (and if possible removal) of invasive species. Therefore, priority should be given to management measures for the regulation of the two herbivore fishes that have led to severe deforestation of the infralittoral rocky shores of Santorini Island, as well as other locations in the southern Aegean Sea (Bianchi *et al.*, 2014; Vergés *et al.*, 2014; authors' unpublished data).

The involvement of key stakeholders throughout the MPA establishment process in Santorini is pivotal in reinforcing compliance and success. Several public discussion events and consultation meetings have been organized thus far aiming to inform local authorities and the general public, to achieve consensus for protection and, more importantly, to enhance active engagement in the planning process. Taking into account both ecological (as highlighted in this study) and socioeconomic requirements (as later expressed by various key stakeholders), there is now general agreement and common interest in the establishment of an MPA along a ~9.8 km coastal stretch of Akrotiri Peninsula (~4.21 km^2). This is a slow, ongoing process mostly due to labyrinthine bureaucratic and legislative issues, which nevertheless allows adequate time for the local community to adjust to this novel perspective.

Acknowledgements

The first two authors coordinated this study; the remaining authors are presented in alphabetical order.

This project was initiated by Cousteau Divers (www.cousteaudivers.org) and sponsored by the Stavros Niarchos Foundation. Thanks are due to Navy's Waterworld and Santorini Dive Centres for kindly providing invaluable field and technical support. We greatly appreciate the constructive input of two anonymous reviewers, who substantially helped us improve this manuscript.

References

Agardy, T., 2000. Information needs for marine protected areas: Scientific and societal. *Bulletin of Marine Science,* 66 (3), 875-888.

Alcoverro, T., Duarte, C.M., Romero, J., 1995. Annual growth dynamics of *Posidonia oceanica*: contribution of large scale versus local factors to seasonality. *Marine Ecology Progress Series*, 120, 203-210.

Aronov, A., Goren, M., 2008. Ecology of the mottled grouper (*Mycteroperca rubra*) in the eastern Mediterranean. *Electronic Journal of Ichthyology*, 2, 43-55.

Bianchi, C.N., Corsini-Foka, M., Morri, C., Zenetos, A., 2014. Thirty years after: dramatic changes in the coastal marine ecosystems of Kos Island (Greece), 1981-2013. *Mediterranean Marine Science*, 15, 482-497.

Bianchi, C.N., Morri, C., Chiantore, M., Montefalcone, M., Parravicini, V. *et al.,* 2012. Mediterranean Sea biodiversity between the legacy from the past and a future of change. p. 1-55. In: *Life in the Mediterranean Sea: A look at habitat changes.* Stambler, N. (Ed). Nova Science Publishers, New York.

Boudouresque, C.F., Bernard, G., Bonhomme, P., Charbonnel, E., Diviacco, G. *et al.,* 2006. *Preservation et conservation des herbiers a Posidonia oceanica*. RaMoGe Publication, Monaco, 202 pp.

Bulleri, F., Benedetti-Cecchi, L., Cinelli, F., 1999. Grazing by the sea urchins *Arbacia lixula* L. and *Paracentrotus lividus* Lam. in the Northwest Mediterranean. *Journal of Experimental Marine Biology and Ecology*, 241, 81-95.

Campbell, S.J., Hoey, A.S., Maynard, J., Kartawijaya, T., Cinner, J. *et al.,* 2012. Weak compliance undermines the success of no-take zones in a large government-controlled marine protected area. *PLoS ONE*, 7 (11), e50074.

Claudet, J., Pelletier, D., Jouvenel, J.Y., 2006. Assessing the effect of MPA on a reef fish assemblage in a NW Mediterranean reserve: identifying community based indicators. *Biological Conservation,* 130, 349-369.

Cousteau, P.-Y., Giakoumi, S., Sala, E., 2010. *Creation of a marine reserve in Santorini*. Proposal submitted at the Prefecture of Cyclades, 11 pp.

Daw, T., Brown, K., Rosendo, S., Pomeroy, R., 2011. Applying the ecosystem services concept to poverty alleviation: the need to disaggregate human well-being. *Environmental Conservation*, 38, 370-379.

Day, J., Dudley, N., Hockings, M., Holmes, G., Laffoley, D. *et al.,* 2012. *Guidelines for applying the IUCN Protected Area Management Categories to Marine Protected Areas*. IUCN, Gland, Switzerland, 36 pp.

DeMartini, E.E., Friedlander, A.M., Sandin, S.A., Sala, E., 2008. Differences in fish-assemblage structure between fished and unfished atolls in the northern Line Islands, central Pacific. *Marine Ecology Progress Series,* 365, 199-215.

Ferreira, A., Seixas, S., Marques, J.C., 2015. Bottom-up management approach to coastal marine protected areas in Portugal. *Ocean & Coastal Management*, 118, 275-281.

Francour, P., Ganteaume, A., Poulain, M., 1999. Effects of boat anchoring in *Posidonia oceanica* seagrass beds in the Port-Cros National Park (north-western Mediterranean Sea). *Aquatic Conservation: Marine and Freshwater Ecosystems,* 9, 391-400.

Giakoumi, S., 2014. Distribution patterns of the invasive herbivore *Siganus luridus* (Rüppell, 1829) and its relation to native benthic communities in the central Aegean Sea, Northeastern Mediterranean. *Marine Ecology,* 35, 96-105.

Giakoumi, S., Kokkoris, G.D., 2013. Effects of habitat and substrate complexity on shallow sublittoral fish assemblages in the Cyclades Archipelago, North-eastern Mediterranean Sea. *Mediterranean Marine Science*, 14 (1), 58-68.

Giakoumi, S., Cebrian, C., Kokkoris, G.D., Ballesteros, E., Sala, E., 2012. Relationships between fish, sea urchins and macroalgae: The structure of shallow rocky sublittoral communities in the Cyclades, Eastern Mediterranean. *Estuarine, Coastal and Shelf Science*, 109, 1-10.

Guidetti, P., Sala, E., 2007. Community-wide effects of marine reserves in the Mediterranean Sea. *Marine Ecology Progress Series*, 335, 43-56.

Guidetti, P., Milazzo, M., Bussotti, S., Molinari, A., Murenu, M. *et al.,* 2008. Italian marine reserve effectiveness: Does enforcement matter? *Biological Conservation*, 141, 699-709.

Guidetti, P., Bussoti, S., Pizzolante, F., Ciccolella, A., 2010. Assessing the potential of an artisanal fishing co-management in the Marine Protected Area of Torre Guaceto (southern Adriatic Sea, SE Italy). *Fisheries Research*, 101 (3), 180-187.

Guidetti, P., Baiata, P., Ballesteros, E., Di Franco, A., Hereu, B. *et al.,* 2014. Large-scale assessment of Mediterranean Marine Protected Areas effects on fish assemblages. *PLoS ONE*, 9 (4), e91841.

Harmelin-Vivien, M.L., Bitar, G., Harmelin, J.G., Monestiez, P., 2005. The littoral fish community of the Lebanese rocky coast (eastern Mediterranean Sea) with emphasis on Red Sea immigrants. *Biological Invasions*, 7 (4), 625-637.

HCMR, 2007. *Study of the short-term effects of the pollution caused by the accident of the cruise ship Sea Diamond in Athinios bay in Santorini Island*. HCMR Technical report, 61 pp.

HCMR, 2008. *Study of the effects of the pollution caused by the accident of the cruise ship Sea Diamond in Athinios bay in Santorini Island, 1st year Technical report (measurements period: May-November 2007)*. HCMR Technical report (in Greek), 94 pp.

HCMR, 2009. *Study of the effects of the pollution caused by the accident of the cruise ship Sea Diamond in Athinios bay in Santorini Island, 2nd year Technical report (measurements period: May-November 2008)*. HCMR Technical report (in Greek), 66 pp.

HCMR, 2010. *Study of the effects of the pollution caused by the accident of the cruise ship Sea Diamond in Athinios bay in Santorini Island, 3rd year Technical report (measurements period: October 2009-May 2010)*. HCMR Technical report (in Greek), 62 pp.

HCMR, 2011. *Study of the effects of the pollution caused by the accident of the cruise Sea Diamond in Athinios bay in Santorini Island, 4th year Technical report (measurements period: November 2010-May 2011)*. HCMR Technical report (in Greek), 82 pp.

HCMR, 2012. *Study of the effects of the pollution caused by the accident of the cruise Sea Diamond in Athinios bay in Santorini Island, 5th year Technical report (measurements period: November 2011-May 2012)*. HCMR Technical report (in Greek), 61 pp.

Jennings, S., 2000. Patterns and prediction of population recovery in marine reserves. *Reviews in Fish Biology and Fisheries*, 10 (2), 209-231.

Katsanevakis, S., Levin, N., Coll, M., Giakoumi, S., Shkedi, D. *et al.,* 2015. Marine conservation challenges in an era of economic crisis and geopolitical instability: the case of the Mediterranean Sea. *Marine Policy*, 51, 31-39.

La Messa, G., Vacchi, M., 1999. An analysis of the coastal fish assemblage of the Ustica Island Marine Reserve (Mediterranean Sea). *Marine Ecology*, 20, 147-165.

La Mesa, G., Molinari, A., Gambaccini, S., Tunesi, L., 2011. Spatial pattern of coastal fish assemblages in different habitats in North-western Mediterranean. *Marine Ecology*, 32 (1), 104-114.

Leleu, K., Remy-Zephir, B., Grace, R., Costello, M.J., 2012. Mapping habitats in a marine reserve showed how a 30-year trophic cascade altered ecosystem structure. *Biological Conservation*, 155, 193-201.

Lester, S.E., Halpern, B.S., Grorud-Colvert, K., Lubchenco, J., Ruttenberg, B.I. *et al.,* 2009. Biological effects within no-take marine reserves: a global synthesis. *Marine Ecology Progress Series*, 384 (2), 33-46.

Lubchenco, J., Grorud-Colvert, K., 2015. Making waves: The science and politics of ocean protection. *Science*, 340, 382-383.

Micheli, F., Levin, N., Giakoumi, S., Katsanevakis, S., Abdulla, A. *et al.,* 2013. Setting priorities for regional conservation planning in the Mediterranean Sea. *PLoS ONE,* 8 (4), e59038.

Montefalcone, M., 2009. Ecosystem health assessment using the seagrass *Posidonia oceanica*: a review. *Ecological Indicators*, 9, 595-604.

Montefalcone, M., Albertelli, G., Morri, C., Bianchi, C.N., 2007. Urban seagrass: status of *Posidonia oceanica* facing the Genoa city waterfront (Italy) and implications for management. *Marine Pollution Bulletin*, 54, 206-213.

Montefalcone, M., Albertelli, G., Morri, C., Parravicini, V., Bianchi, C.N., 2009. Legal protection is not enough: *Posidonia oceanica* meadows in marine protected areas are not healthier than those in unprotected areas of the north-west Mediterranean Sea. *Marine Pollution Bulletin*, 58, 515-519.

Montesanto, B., Panayotidis, P., 2001. The *Cystoseira* spp. communities from the Aegean Sea (NE Mediterranean). *Mediterranean Marine Science*, 2 (1), 57-67.

Nomikou, P., Parks, M.M., Papanikolaou, D., Pyle, D.M., Mather, T.A. *et al.,* 2014. The emergence and growth of a submarine volcano: The Kameni islands, Santorini (Greece). *Geological Research Journal*, 1, 8-18.

Orfanidis, S., Panayotidis, P., Stamatis, N., 2001. Ecological evaluation of transitional and coastal waters: a marine benthic macrophytes based model. *Mediterranean Marine Science*, 2 (2), 45-65.

Osenberg, C.W., Shima, J.S., Miller, S. L., Stier, A.C., 2011. Assessing effects of marine protected areas: confounding in space and possible solutions. p. 143-167. In: *Marine protected areas: a multidisciplinary approach*. Claudet, J. (Ed). Cambridge University Press, New York.

Pennewiss, S., 2004. The old man and the sea: a field study of change in the Greek fishing industry based on interviews with fishermen on the Island of Santorini. *International Journal of Entrepreneurship and Small Business*, 1 (1-2), 206-210.

Pergent, G., Pergent-Martini, C., Boudouresque, C.F., 1995. Utilisation de l'herbier à *Posidonia oceanica* comme indicateur biologique de la qualité du milieu littoral en Méditerranée: état des connaissances. *Mésogée*, 54, 3-27.

Pergent, G., Pergent-Martini, C., Bein, A., Dedeken, M., Oberti, P. *et al.,* 2015. Dynamic of *Posidonia oceanica* seagrass meadows in the northwestern Mediterranean: Could climate change be to blame? *Comptes Rendus Biologies*, 338 (7), 484-493.

Pergent-Martini, C., Leoni, V., Pasqualini, V., Ardizzone, G.D., Balestri, E. *et al.,* 2005. Descriptors of *Posidonia oceanica* meadows: use and application. *Ecological Indicators*, 5, 213-230.

PISCO (Partnership for Interdisciplinary Studies of Coastal Oceans), UNS (University of Nice Sophia Antipolis), 2016. *The Science of Marine Protected Areas (3rd edition, Mediterranean)*. www.piscoweb.org, 22 pp.

Pollnac, R., Christie, P., Cinner, J.E., Dalton, T., Daw, T.M. *et al.,*2010. Marine reserves as linked social–ecological systems. *Proceedings of the National Academy of Sciences*, 107 (43), 18262-18265.

Sala, E., Zabala, M., 1996. Fish predation and the structure of the sea urchin *Paracentrotus lividus* populations in the NW Mediterranean. *Marine Ecology Progress Series*, 140, 71-81.

Sala, E., Boudouresque, C.F., Harmelin-Vivien, M., 1998. Fishing, trophic cascades, and the structure of algal assemblages: evaluation of an old but untested paradigm. *Oikos*, 82, 425-439.

Sala, E., Kizilkaya, Z., Yildirim, D., Ballesteros, E., 2011. Alien marine fishes deplete algal biomass in the eastern Mediterranean. *PLoS ONE*, 6, e17356.

Sala, E., Ballesteros, E., Dendrinos, P., Di Franco, A., Ferretti, F. *et al.,* 2012. The structure of Mediterranean rocky reef ecosystems across environmental and human gradients, and conservation implications. *PLoS ONE*, 7 (2), e32742.

Salomidi, M., 2009. *Rapid Assessment of the Coastal Ecological Status (RACES) by the use of visual sampling of the upper infralittoral phytobenthic communities: a step towards the implementation of the Water Framework Directive*. PhD Thesis. University of the Aegean, Mytilene, Greece, 227 pp.

Salomidi, M., Katsanevakis, S., Borja, A., Brackenman, U., Damalas, D. *et al.,* 2012. Assessment of goods and services, vulnerability, and conservation status of European seabed biotopes: a stepping stone towards ecosystem based marine spatial management. *Mediterranean Marine Science*, 13 (1), 49-88.

Sandin, S.A., Smith, J.E., DeMartini, E.E., Dinsdale, E.A., Donner, S.D. *et al.,* 2008. Baselines and degradation of coral reefs in the northern Line Islands. *PLoS ONE*, 3 (2), e1548.

Stergiou, K.I., 2002. Overfishing, tropicalization of fish stocks, uncertainty and ecosystem management: reshaping Ockham's razor. *Fisheries Research*, 55, 1-9.

UNEP/MAP-RAC/SPA, 2011. *Draft Guidelines for the Standardization of Mapping and Monitoring Methods of Marine Magnoliophyta in the Mediterranean*. RAC/SPA Publication, UNEP (DEPI) / MED WG 359/9, 63 pp.

Vergés, A., Tomas, F., Cebrian, E., Ballesteros, E., Kizilkaya, Z. *et al.,* 2014. Tropical rabbitfish and the deforestation of a warming temperate sea. *Journal of Ecology*, 102 (6), 1518-1527.

Wadih, H.E., 2005. *Identifying and assessing tourism impact factors on localities and their nations: with illustrations from Santorini*. MSc Thesis. University of Cincinnati, Cincinnati, USA, 105 p.

Willis, T.J., Millar, R.B., Babcock, R.C., Tolimieri, N., 2003. Burdens of evidence and the benefits of marine reserves: putting Descartes before des horse? *Environmental conservation*, 30 (2), 97-103.

Appendix

Table 1. List of the *Posidonia oceanica* (editor's choice) metrics studied, anticipated responses to different impacts, and sampling protocols.

Metrics	Impact or stress	Expected Response	Method
Meadow Cover (%)	Reduction of light availability. Burial. Direct elimination due to trawl fishing, boat anchoring, coastal construction, etc.	Vegetal cover decrease	Estimated by the non-destructive Line Intercept Transect (LIT) methodology (Montefalcone *et al.*, 2007) along three transect lines of 25 m placed in three random directions. The observer recorded the intercept to the nearest centimetre corresponding to the point where the key attributes (e.g. *Posidonia* bed, sandy bottom, dead matte, etc.) changed under the line. Meadow Cover (R%) is calculated using the following formula: $R\% = \Sigma(Lx/25 \times 100)$; where the length of each key attribute (Lx) is the distance between two recorded intercepts at each LIT and is calculated by subtraction.
Shoot density (shoots m^{-2})	Reduction of light availability. Burial. Direct elimination due to trawl fishing, boat anchoring, coastal construction, etc.	Shoot mortality (Shoot density decrease)	Shoot number was counted in 20 (20 × 20 cm) replicate quadrats randomly set along the three replicate line transects at 15 m depth (4 quadrats per transect) (Boudouresque *et al.*, 2006).
Plagiotropic growth of rhizomes (%)	Reduction of light availability. Sediment resuspension. Burial. Boat anchoring, coastal construction, etc.	Increase of the percentage of plagiotropic rhizomes	In situ observation of plagiotropic rhizomes in the same 20 replicate quadrats (20 × 20cm) used for shoot density (Boudouresque *et al.*, 2006).
Lower Limit Typology	Reduction of light availability. Burial. Direct elimination due to trawl fishing, boat anchoring, coastal construction, etc.	Change to different type of LL	In situ observation of the presence of dead *P. oceanica* shoots (dead matte) and plagiotropic rhizomes over the LL. Five types of the LL have been described (progressive, erosive, sharp, sparse and regressive) (Pergent *et al.*, 1995). *
Conservation Index (CI)	Reduction of light availability. Burial. Direct elimination due to trawl fishing, boat anchoring, coastal construction, etc.	Decrease to lower values	Calculation of the CI applied to data obtained using the LIT method, using the following formula: $CI = P / (P + D)$, where P is the % cover of living *P. oceanica* plants and D is the % cover of dead matte (Montefalcone, 2009).

* The results of the LL typology were assigned to five status categories: progressive and erosive (P) = high, sharp high cover (S+) = good, sharp low cover (S-) = moderate, sparse = poor status, regressive = bad status) (Pergent *et al.*, 2015).

Table 2. Assessment of the vitality of *Posidonia oceanica* meadows, based on the applied set of metrics (UNEP/MAP-RAC/SPA, 2011, modified).

Metric	***High*** **(5)**	***Good*** **(4)**	***Normal*** **(3)**	***Poor*** **(2)**	***Bad*** **(1)**
Shoot density (shoots m^{-2})	>492	492-372	372-253	253-134	<134
Plagiotropic growth of rhizomes (%)	-	-	<30	30-70	>70
Lower Limit Typology	Progressive / Erosive	Sharp+	Sharp-	Sparse	Regressive
Conservation Index	> 0.9	0.9 - 0.7	0.7 - 0.5	0.5 - 0.3	< 0.3

The vitality index corresponds to the average of the four metrics (max= 5, min= 1).

Table 3. Checklist for taxa recorded at the upper infralittoral (0-1 m) rocky shores across the study area (18 sampling stations) with respective mean % cover value, standard error (± SE), frequency of occurrence (f), and Ecological State Group (according to Orfanidis *et al*., 2001).

Taxa/Morphological Group	Mean	SE	f	ESG
Amphiroa rigida J.V. Lamouroux	0.011	0.008	2	I
Anadyomene stellata (Wulfen) C. Agardh	0.349	0.163	7	I
Caulerpa cylindracea Sonder	0.139	0.096	3	II
Chrysophyta	0.176	0.149	3	II
Corallina sp.	1.022	0.487	8	I
Cystoseira spp.	42.822	4.828	18	I
Dictyopteris polypodioides (De Candolle) Lamouroux	0.006	0.006	2	II
Dictyota spp.	0.017	0.009	3	II
Encrusting red algae	6.928	1.602	18	I
Flabellia petiolata (Turra) Nizamuddin	0.154	0.154	1	I
Jania spp.	18.854	2.349	18	I
Laurencia complex	6.338	2.551	11	II
Padina pavonica (Linnaeus) Thivy	0.076	0.037	8	I
Sargassum sp.	2.373	1.921	7	I
Titanoderma trochanter (Bory) Benhissoume, Boudouresque, Perret-Boudouresque *et* Verlaque	0.565	0.489	3	I
Turf Algae	20.046	2.882	18	II
Valonia sp.	0.006	0.006	1	II